COMPARATIVE FLORAL BIOLOGY OF *PENSTEMON EATONII* AND *PENSTEMON CYANANTHUS* IN CENTRAL UTAH: A PRELIMINARY STUDY

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Abstract. — A comparison of the floral visitors of two closely related plant species, *Penstemon cyananthus* and *P. eatonii*, suggests that flower shape and color may affect the number and type of pollinators, and the ability of the plant to set fruit. *Penstemon cyananthus*, which is most attractive to hymenopteran visitors, has a blue flower, large in diameter, that is positioned as a convenient "landing pad." Although many types of insects visit the flower, the transport of pollen directly to flowers of another individual of the same species is somewhat inefficient, since fruiting success is low (66.7 percent). The tubular red flowers of *P. eatonii* are narrow and droop downward from the stem. The nectar is accessible to a specific and well-adapted visitor, the hummingbird. This less promiscuous, bird-pollinated species sets fruit more successfully (82.4 percent) than *P. cyananthus*.

Observations of animal visitors to flowers suggest that the broad range of phenology, size, structure, color, and odor evident among flowers of any complex plant community is related to the size, morphology, behavior, and sensory acuity of the animals visiting the flowers. It has been observed, for instance, that nocturnal blooming flowers are specially adapted to night-flying insects or bats (Faegri and Pijl 1971). Bees appear to be more influenced by flower shape than color. Bees also have appendages specialized for collection and transport of pollen, since pollen is an important food item for their offspring. Accordingly, flowers visited by bees may be white, blue, or yellow, but commonly offer a generous reward of both nectar and pollen (Proctor and Yeo 1972, Raven, Evert, and Curtis 1976). Flowers whose most frequent visitors are nonhovering individuals such as bees are usually so structured as to provide a "landing pad" near the flower's reproductive parts and nectar or pollen "reward" (Free 1970).

In view of the fact that few insects are believed able to distinguish red (Raven, Evert, and Curtis 1976), it seems significant that red flowers worldwide are regularly visited by birds, known to be more stimulated by that color than any other (Faegri and Pijl 1971). It is an interesting and probably not unrelated fact that red flowers, unlike most flowers of other colors, are essentially odorless (Grant 1966). Significantly, insects have keen olfactory senses, but those faculties in birds tend to be poorly developed (Proctor and Yeo 1972, Faegri and Pijl 1971). The corolla of many flowers visited by birds is typically tubular and narrow and without a landing platform, excluding all but the smallest insect intruders (Raven, Evert and Curtis 1976). Clearly, flowers that are tubular, red, and odorless should offer minimal attraction to insects, specifically nonhovering insects, but should be highly attractive to birds (Boyd and Brown 1978).

Phenological, structural, color, and odor differences among the flowers of any particular complex plant community undoubtedly increase the degree of fidelity between particular flower types and specific insects. Since flowering periods of different species in a common plant community often overlap, flower-pollinator fidelity should enhance reproductive success of plant species having such flowering overlap. Plants able to selectively entice pollinators should be more successful in the distribution of their pollen. The animal visitor should simply find it more profitable to visit nonpromiscuous flowers, since there is a greater probability that such flowers will yield a reward on any given visit. Promiscuous pollinators would be particularly detrimental to the reproductive success of rare to moderately common plants that are obligate outcrossers, and that flower simulta-

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neously with a variety of other species, since pollen of a given species could be expected to be largely dislodged from the body of the promiscuous pollinator before it encountered another individual of that plant species (Levin and Anderson 1970).

Evidence suggests that, by chance mutation, plants gradually develop characteristics attractive to the most consistent pollinators in the community. Surviving individuals of the species become specialized for visits from the more efficient pollinators. Tantalizing odors beckon hungry insects, and brightly colored corollas are a signal to the pollinators of the presence of a nectar reward. These forms of advertisement attract pollinators, and thereby accomplish a more efficient spread of pollen.

STATEMENT OF THE PROBLEM

Few studies have been made of the comparative floral biology of two species of the same genus growing in a common environment and flowering simultaneously. The purpose of this study is to compare the floral morphology, insect visitors, and fruit set of two closely related species, *Penstemon eatonii* Gray and *Penstemon cyananthus* Hook. At the site studied, these species grow in close proximity, although individuals of *P. cyananthus* are approximately twice as numerous. I have tested the following hypotheses: (a) Corolla size and color affect the number and types of pollinators. (b) *P. eatonii*, with a red, narrow corolla tube, will attract fewer insects and will be visited by hummingbirds. (c) *P. cyananthus*, with a broader, blue corolla, will be more promiscuous, attracting a variety of insects. (d) The less promiscuous, bird-pollinated species will set fruit more successfully.

MATERIALS AND METHODS

Penstemon eatonii plants produce from 5–10 inflorescences, each approximately 50 cm in length. Narrow tubular corollas hang downward along the upright stem. The five-lobed corolla is red. Four fertile stamens lie within the corolla tube, and one sterile stamen protrudes beyond the corolla orifice (Fig. 1A).

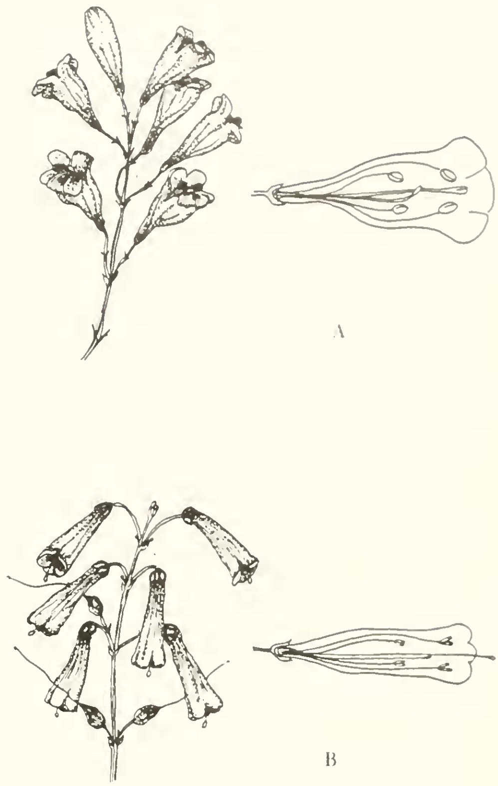

Fig. 1A. *Penstemon cyananthus* flower shape and arrangement of reproductive organs (above); 1B. *Penstemon eatonii* flower shape and arrangement of reproductive organs.

Penstemon cyananthus generally produces four to five times as many infloresenses as *P. eatonii*, each approximately 45 cm in length. Each blue, five-lobed corolla is displayed at an ascending angle from the stem and has fused petals and five stamens, four fertile and one sterile. Two stamens are as long as the petals, but the other two are only two-thirds that length (Fig. 1B).

The data were collected 29 June, and 2 July 1979 on the west face of Mount Timpanogos, in Battlecreek Canyon, near Pleasant Grove, Utah. A small stream flows through the relatively dry study site. Some of the major contributors to the vegetation of the area are: sagebrush (*Artemisia tridentata* Nutt.), rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britt.), poison ivy (*Toxicodendron radicans* L.), scrub oak (*Quercus gambelii* Nutt.), big tooth maple (*Acer gradidentatum* Nutt.), chokecherry (*Prunus virgi-

niana L.), squawbush (*Rhus trilobata* Nutt.), and various grasses.

Observations of the plants were made daily in the first half of each hour from 0730 to 1800 hours. On 29 June *P. cyananthus* was observed during the first hour, *P. eatonii* during the second, and so on throughout the day. On 2 July the observation order was reversed. The two plants observed during these time periods were within four feet of each other.

Fruit set data were collected 14 July 1979, about 0.4 km down the canyon from the first observation site. Individuals of each species were randomly selected and checked for height, spent flowers, developing fruit, open flowers, and buds. Ten stems of each of 8 different *P. cyananthus* plants were analyzed. Because of fewer stems per plant, 13 *P. eatonii* individuals with up to 10 stems per plant were also tallied. Of the total flowers that had been produced per inflorescence, both species showed at least 90 percent spent flowers, the remainder of the number consisting of open flowers and buds.

Average fruit set was calculated using the formula:

$$\frac{\text{No. filled fruits}}{\text{No. spent flowers}}$$

Plant nomenclature follows Welsh and Moore (1973). Insect family names are taken from Borror and White (1970). Bird identification is from Robbins, Bruun, and Zim (1966).

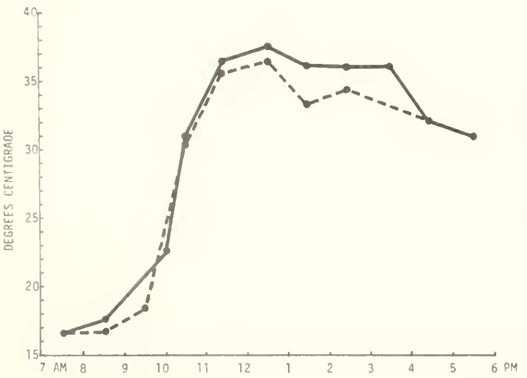

Fig. 2. Temperature readings in degrees Celsius for 29 June (dotted line) and 2 July (solid line).

Results

Insect activity was minimal during the early morning hours, but as air temperature rose, greater numbers and more types of insects appeared. Temperatures for the two days of observation were similar (Fig. 2).

Penstemon cyananthus attracted a greater number of total visitors (153 in two days), and also more insect families (9) than *P. eatonii* (Table 1). Not all insect visitors came to the plant in search of pollen or nectar. Some coleopterans landed on the showy petals as if to rest, making no attempt to enter the flower. Still other types of insects crawled among the stems and leaves. Neither of these types of visitors were recorded as pollinators. The most numerous and determined visitors were hymenopterans in search of pollen (Table 1). Hymenopterans accounted for 85 percent of the visitors and over 89 percent of the flowers visited. Thirteen percent of the visitors to *P. cyananthus* were lepidopterans and the remaining 2 percent were dipterans.

Penstemon eatonii attracted fewer insect visitors (23) or 15 percent as many as *P. cyananthus*. The visitors that were observed be-

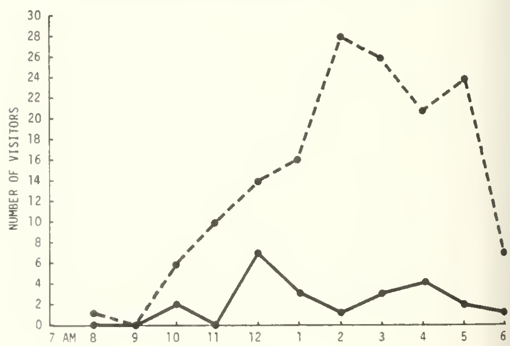

Fig. 3. Hourly distribution of individual flower visitors to *Penstemon cyananthus* (dotted line) and *P. eatonii* (solid line) throughout the observation period.

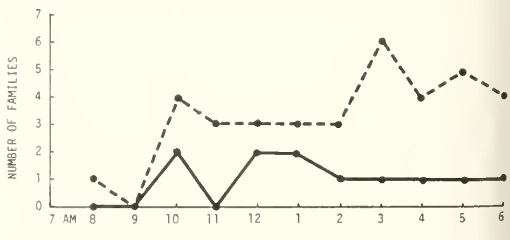

Fig. 4. Hourly distribution of insect families that visited *Penstemon cyananthus* (dotted line) and *P. eatonii* (solid line) throughout the observation period.

longed to three hymenopteran families. During the heat of the day, when the greater numbers of insects were actively foraging, 4 or 5 attempted to enter the narrow corolla tube. Few were successful in their efforts. Once during the observation period, a broad-tailed hummingbird visited the plant at 0930, before the temperature had risen above 24 C (75 F). The bird moved systematically down the canyon, stopping at every *P. eatonii* individual within 10 or 20 m of either side of the path. Upon reaching the observation plant, the bird sampled five or six flowers on four of the six stalks, pausing less than one second at each flower. It hovered in the air slightly below each flower (Figs. 3 and 4).

Penstemon cyananthus averaged 66.7 percent fruit set per plant, and *P. eatonii* showed a much higher 82.4 percent (Table 2).

Discussion

The results of this study clearly indicate that the two penstemons considered have de-

Table 1. Activity and presence of each family throughout the observation period. The first (upper) number indicates the number of individual visitors; the second (lower) indicates the total number of flowers visited.

	Hour observed											
Family	8	9	10	11	12	1	2	3	4	5	6	Total
					Penstemon cyananthus							
Apidae[1]	1		1						1			3
	2		3						3			8
Chrysididae[1]				3				3				6
				10				12				22
Halictidae[1]			1		3	5	4	3	2	2	1	21
			1		6	6	4	5	2	3	2	29
Hesperiidae[2]			2	4				6			1	13
			2	7				15			1	25
Megachilidae[1]				3	9	7	16	10	10	18	2	75
				10	25	16	39	26	15	47	5	183
Nymphalidae[2]					2	4						6
					5	6						11
Pieridae[2]										1		1
										1		1
Syrphidae[3]								2		1		3
								2		1		3
Vespidae[1]			2				8	2	8	2	3	25
			11				22	6	26	9	15	89
Total	1		6	10	14	16	28	26	21	24	7	153
	2		17	27	36	28	65	66	46	61	23	370
					Penstemon eatonii							
Formicidae[1]			1									1
			1									1
Halictidae[1]					1	2	1		1		1	12
					5	4	3		7		2	21
Megachilidae[1]					3	1		3		2		9
					4	1		7		5		17
*Trochilidae[4]			1									1
			15									15
Total			2		7	3	1	3	1	2	1	23
			16		9	5	3	7	7	5	2	54

Key to the orders: 1. Hymenoptera; 2. Lepidoptera; 3. Diptera, 4. Apodiformes (*Selasphorus platycercus)

TABLE 2. Percent fruiting success per plant of *Penstemon cyananthus* and *P. eatonii* (Number of fruit/spent flowers/plant). (Difference significant at the .05 level)

Plant	*P. cyananthus* %	*P. eatonii* %
1	84.7	45.5
2	47.5	93.3
3	59.8	73.1
4	47.6	68.5
5	74.8	89.7
6	75.5	90.0
7	69.7	77.4
8		79.3
9		90.8
10		86.1
11		95.4
12		82.4
13		100.0
Average %	66.7	82.4

veloped different ways of attracting pollinators. The narrow red corolla tube of *P. eatonii* physically excludes all but a few small insect visitors, and the absence of odor appears to minimize attractiveness to insect visitors. The absence of any sort of a landing pad hinders the ability of nonhovering visitors to successfully work the flowers. The only obvious diurnal pollinator, a hummingbird, is less frequent but more systematic and specific. That the job of pollination is done more efficiently by such a specific pollinator is suggested by the higher fruit set.

The more promiscuous *P. cyananthus* also enjoys a fairly high fruit set. It does this, however, with larger, more accessible blossoms and with no assurance that its pollinators will be species specific. The flowers are, of necessity, displayed so as to form a convenient landing pad for approaching hymenopterans.

LIMITATIONS

Although the initial implications are clear, these data constitute only preliminary results. Data were collected during daylight hours late in the flowering season, when flowers of both species contained little or no nectar. Only one hummingbird was observed directly during the study, but my presence may have frightened usual avian visitors away. No attempt was made to observe early evening or nocturnal pollinators. The degree to which either species is capable of self-pollination is unknown.

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